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Helping plants to deal with insects: the role of beneficial soil-borne microbes

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Several soil-borne microbes such as mycorrhizal fungi and plant growth-promoting rhizobacteria can help plants to deal with biotic and abiotic stresses via plant growth promotion and induced resistance. Such beneficial belowground microbes interact in a bidirectional way via the plant with aboveground insects such as herbivores, their natural enemies and pollinators. The role of these interactions in natural and agricultural ecosystems is receiving increased attention, and the molecular and physiological mechanisms involved in these interactions should be the focus of more attention. Here, we review the recent discoveries on plant-mediated interactions between beneficial belowground microbes and aboveground insects.

Plant as a linking element

Modern agriculture is facing new challenges in which ecological and molecular approaches are being integrated to achieve higher crop yields while minimising negative impacts on the environment. In this context, enhancing plant growth, plant resistance and biological control of pests are key strategies. Plants have developed direct defences (see Glossary) against insect herbivores and indirect defences to promote the effectiveness of natural enemies of insect herbivores [1]. Hence, plants act as mediators of multitrophic interactions between a wide diversity of attackers and beneficial organisms [1–5]. Moreover, plants also link belowground and aboveground community members [6–9], such as soil-borne microbes and aboveground insects (Figure 1).

Diverse groups of soil-borne microbes (e.g. root endophytic fungi, mycorrhizal fungi, plant growth-promoting fungi and rhizobacteria, and rhizobia) exert positive effects on plant growth and survival through direct and plant-mediated mechanisms [8,10–14]. Two main mechanisms that involve changes in plant physiology can be distinguished: plant growth promotion and induced systemic resistance (ISR) [12,13,15–19]. ISR protects the plant against a broad range of diseases [20–23] and can be triggered by a wide variety of beneficial microbes. A growing body of evidence suggests that different beneficial microbes induce ISR through similar mechanisms [20–23], involving common regulators of plant defences [2,3]. Beneficial microbes also interact with aboveground insects (herbivores, natural enemies and pollinators) via plant-mediated mechanisms, often leading to negative effects on the insect herbivore (Table 1). Plant growth promotion has traditionally been considered the main mechanism underlying microbe–plant–insect interactions, whereas the importance of induced defences has recently emerged and still much is unknown about the role of ISR in such interactions [8,24–26].

Interest in plant-mediated interactions between different organisms in general [5] and in aboveground–belowground plant-mediated interactions has increased [6,7]. Specifically, molecular mechanisms of plant defence have been the focus of increased attention in the past decade [3,25–29]. This has called for integration of the relatively unconnected research fields of plant–microbe and plant–insect interactions [3,30]. Here, we review the recent discoveries on plant-mediated interactions between beneficial belowground microbes and aboveground insects. We will address: (i) which mechanisms are involved in microbe–plant–insect interactions; (ii) how aboveground herbivorous and beneficial insects are affected by belowground microbes; and (iii) how belowground microbes are affected by aboveground herbivory.

Microbes enhancing plant growth

Plant growth promotion was the first beneficial effect known for the symbiosis of plants with mycorrhiza and

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Glossary

Chewing feeders: insects (e.g. caterpillars) that have chewing mouthparts and feed on plant tissue, removing pieces of tissues.
Beneficial soil-borne microbe: microbe that colonises the rhizosphere and that provides a benefit to the plant, such as enhancing plant growth, inducing resistance or directly neutralising detrimental organisms.
Direct defences: plant characteristics that negatively affect the performance of herbivorous insects, such as toxins or thorns, and thereby enhance the fitness of the plant.
Indirect defences: plant characteristics that improve the effectiveness of natural enemies of herbivores, for example through provision of shelter, alternative food or infochemicals, and thereby enhance the fitness of the plant.
Induced systemic resistance (ISR): enhanced resistance of a plant against detrimental organisms, induced by non-pathogenic soil-borne microbes such as plant growth-promoting rhizobacteria and fungi.
**Phloem feeders**: insects (e.g. aphids and whiteflies) that feed on phloem sap with mouthparts modified into a sucking stylet.
Plant hormones: endogenous secondary metabolites such as jasmonic acid or abscisic acid that regulate physiological processes in the plant such as defence and growth.
Priming: change in physiological state that allows the plant to activate defence responses faster and stronger against different attackers, and that can be elicited by living organisms and synthetic compounds.
Rhizosphere: space around plant roots containing a high density of microbes, directly influenced by both roots and microbes.
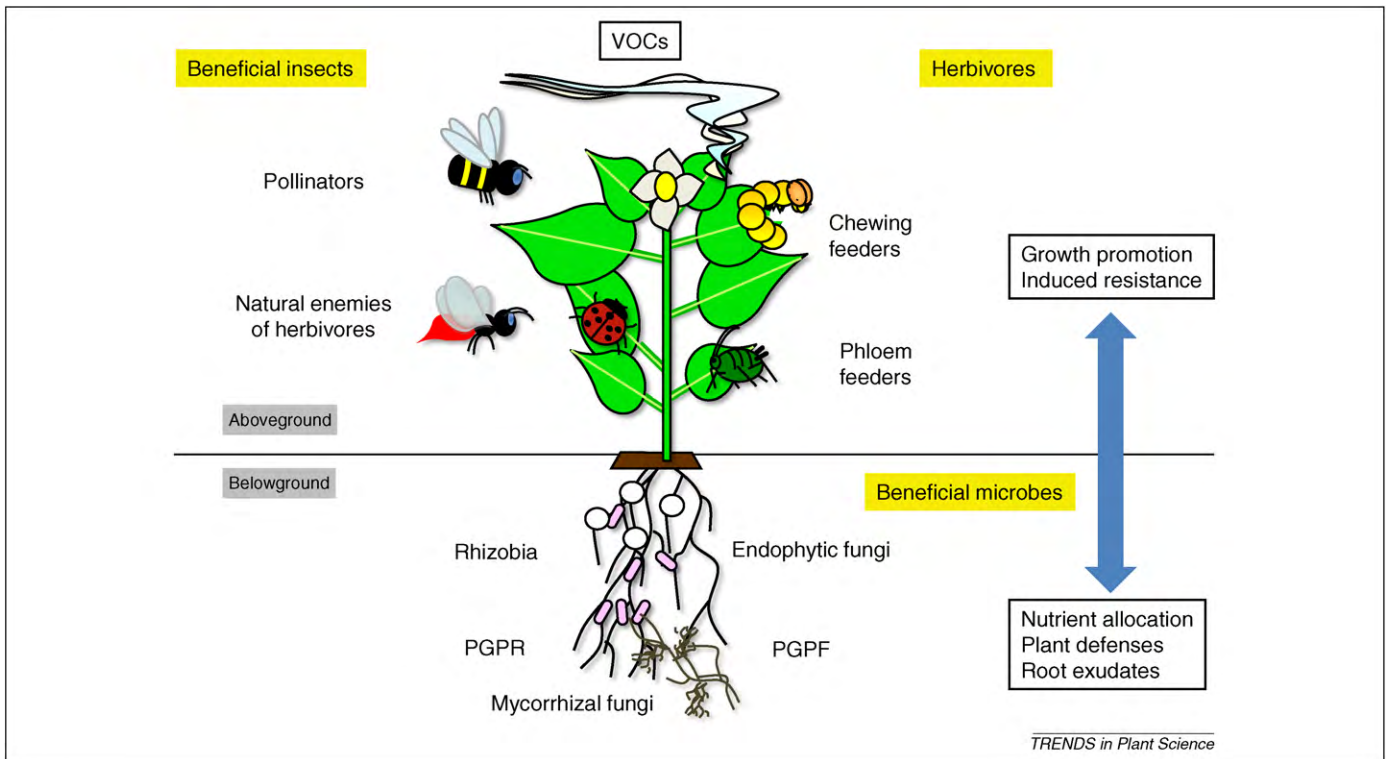
Figure 1. Multitrophic interactions between beneficial microbes belowground and insects aboveground. Different soil-borne microbes induce changes in the plant that affect herbivorous insects, their natural enemies and pollinators. The beneficial microbes enhance plant growth and induce resistance in aerial plant tissues, which both affect herbivore performance. The emission of plant volatile organic compounds (VOCs) is the main cue triggering the attraction of beneficial insects, and this emission changes in response to microbe-plant interactions. Aboveground herbivory affects microbial communities belowground, possibly via changes in nutrient allocation, broad-spectrum induced defences and root exudates.

Table 1. Soil-borne microbes showing a plant-mediated effect on aboveground herbivores

Microbe species	Microbe group[a]	Herbivore insects	Plants	Effect on insect	Refs
Acremonium alternatum	Fungal endophytes	*Plutella xylostella* (C)	Cabbage (*Brassica oleracea*)	Negative	[106]
Acremonium strictum	Fungal endophytes	*Helicoverpa armigera* (C), *Trialeurodes vaporariorum* (P), *Aphis fabae* (P)	Tomato, broad bean (*Vicia faba*)	Negative	[63,107–109]
Rhizobium leguminosarum	Rhizobia	*Spodoptera littoralis* (C), *Myzus persicae* (P)	White clover	Positive/ no effect	[39]
Bacillus amyloquefaciens	PGPR	*Bemisia argentifolii* (P), *Myzus persicae* (P)	Tomato, sweet pepper (*Capsicum annuum*)	Negative/ no effect	[37,110]
Bacillus pumilus	PGPR	*Acalymma vittatum* (C), *Diabrotica undecimpunctata* (C), *Bemisia argentifolii* (P)	Cucumber (*Cucumis sativus*), tomato	Negative	[45,110,111]
Bacillus subtilis	PGPR	*Bemisia argentifolii* (P), *Bemisia tabaci* (P), *Myzus persicae* (P)	Tomato, sweet pepper	Negative/ no effect	[26,37,110]
Flavomonas oryzihabitans	PGPR	*Acalymma vittatum* (C), *Diabrotica undecimpunctata* (C)	Cucumber	Negative	[45]
Pseudomonas fluorescens	PGPR	*Spodoptera exigua* (C), *Cnaphalocrocis medinalis* (C), *Pieris rapae* (C), *Amrasca biguttula biguttula* (P), *Aphis gossypii* (P), *Myzus persicae* (P)	*Arabidopsis*, rice, okra (*Abelmoschus esculentus*)	Negative/ no effect	[25,53,57,58,112]
Pseudomonas putida	PGPR	*Acalymma vittatum* (C), *Diabrotica undecimpunctata* (C)	Cucumber	Negative	[45]
Serratia marcesens	PGPR	*Acalymma vittatum* (C), *Diabrotica undecimpunctata* (C)	Cucumber	Negative	[45]

Abbreviations: chewing feeder (C); phloem feeder (P).
[a]References to mycorrhizal fungi are not cited owing to limited space, for information see [11,64,67].

nitrogen-fixing bacteria, whereas knowledge on such phenomena related to plant growth-promoting rhizobacteria (PGPR), root endophytic fungi and plant growth-promoting fungi (PGPF) has emerged more recently [20]. Beneficial effects on plant growth have a high relevance for agricultural ecosystems because they reduce the need for fertilisers, leading to a decrease in pollution of agricultural soils and water [15,19]. For instance, *Trichoderma* spp. are PGPF that are commercially available and are widely used in agriculture. In addition to their plant growth-promoting effect, they induce systemic resistance against microbial pathogens and act as a biological control agent of such pathogens [17,18,22]; however, the plant-mediated effects of PGPF on insects have never been studied.

The microbe-mediated stimulation of plant growth can be explained by improved plant nutrition and increased tolerance to biotic and abiotic stress. Improved plant nutrition occurs through increasing the uptake and concentration of a variety of nutrients (e.g. phosphorus), solubilising plant nutrients unavailable to plants in certain soils (e.g. rock phosphate) and fixing atmospheric nitrogen. Some microbes can also synthesise plant hormones that promote plant growth (e.g. indole-3-acetic acid, cytokinins, auxines and gibberellins) [13,31] and can increase aboveground photosynthesis through the modulation of endogenous sugar and ABA signalling [32]. Additionally, soil-borne microbes can enhance plant tolerance to abiotic stresses, such as drought, salt stress and the presence of heavy metals in the soil [15,19,33,34].

The plant growth-promoting effect of soil-borne microbes has been shown to affect plant–insect interactions, resulting in a benefit for the insect and/or for the plant. Enhanced plant growth translates into an increased food supply for herbivores. Additionally, the improvement of nutrient composition increases plant nutritional quality, which affects insect performance at several trophic levels [1,35]. Both chewing insects and phloem feeders benefit from the higher content of nitrogen and other limiting nutrients in plant tissues and phloem sap, respectively [1]. Surprisingly, to date, no studies have analysed the effect of beneficial soil-borne microbes on phloem sap composition.

Plants interacting with beneficial microbes can also benefit from an increase in tolerance to herbivory [24,36]. By improving nutrient and water uptake, beneficial microbes can facilitate the regrowth of tissues after herbivory, thus promoting plant tolerance, which is reflected in compensation of the loss of plant biomass or yield in the presence of herbivores [37–39]. This important aspect has not yet been the focus of much attention in studies on plant–microbe interactions.

Microbes inducing systemic resistance
Many soil-borne microbes have the ability to induce plant resistance in systemic tissues, a process termed ISR. Traditionally, ISR is known to be triggered by PGPR and particularly by *Pseudomonas* and *Bacillus* spp. [20,21,40] but recent studies show that ISR can also be elicited by mycorrhizal fungi [17,41], endophytic fungi [42] and PGPF [18,22]. The effectiveness of ISR has been proven in many plant species against pathogenic bacteria,

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Box 1. Molecular mechanisms of induced systemic resistance in *Arabidopsis*

Colonisation of the roots of *Arabidopsis* by beneficial microbes such as *Pseudomonas fluorescens* triggers an induced systemic resistance (ISR) response that is effective against a broad range of attackers [20,21,25]. The first step in the activation of ISR is the recognition of the beneficial microbes through microbe-associated molecular patterns (MAMPs). These compounds include cell surface molecules, such as flagellin and lipopolysaccharides, or compounds that are excreted by the microbe, such as Fe^{3+}-chelating siderophores, antibiotics, biosurfactants and even volatile organic compounds [20,21,93]. Upon recognition, the transcription factor gene *MYB72* is activated in the roots. Mutant *myb72* plants do not mount an ISR response in the leaves, neither upon colonisation by ISR-inducing PGPR nor upon colonisation by ISR-inducing *Trichoderma* PGPF [22,94], indicating that the transcription factor MYB72 plays an essential role in the onset of ISR. Systemic activation of ISR in the leaves requires an intact response to the plant hormones JA and ET, and the defence regulatory protein NPR1 [20–22,42,95]. ISR-inducing agents typically do not trigger direct changes in defence-related gene expression in aboveground plant parts but prime the leaf tissue for a faster and stronger response to pathogen and insect attack [25,96]. The transcription factor MYC2, which plays a key role in the regulation of JA-responsive gene expression, has recently been shown to play an important regulatory role in PGPR-mediated priming for enhanced defence in *Arabidopsis* [97,98].

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fungi, viruses, nematodes and recently also against insects [25,41–45]. ISR has some characteristics that distinguish it from other types of induced resistance (Box 1): it is induced by non-pathogenic microbes upon interaction with the roots of the plant; it is mediated by priming (Box 2) of defence genes that show a higher expression systemically in the leaves only after pathogen or insect attack; and it often involves responsiveness of the plant to the plant hormones jasmonic acid (JA) and ethylene (ET) [20,21]. Nevertheless, the levels of these hormones remain unchanged, suggesting that ISR is based on increased sensitivity to plant hormones rather than on increased production of such hormones [21].

Box 2. Priming for enhanced defences and its potential in agriculture

Priming is a phenomenon that provides plants with an enhanced capacity to rapidly and effectively mount defence responses to biotic and abiotic stresses [96]. Priming can be elicited by beneficial microbes, but also by pathogens, herbivores and selected synthetic compounds such as benzothiadiazole (BTH) and β-aminobutyric acid (BABA) [96,99,100]. Typically, priming is characterised by accelerated defence-related gene expression once primed plants are attacked by a pathogen or an insect, resulting in an enhanced level of resistance against the invader. This enhanced resistance is effective against a broad spectrum of attackers. The molecular basis of priming is poorly understood, but recent advances in the field of priming demonstrate that the accumulation of latent defence-related transcription factors [97], MAP kinases [101] and secondary metabolites such as azelaic acid [102] and volatile organic compounds [99] can play a role in the establishment of the primed state. Expression of constitutive, and to a lesser extent induced defences, is costly for the plant and has negative consequences on plant fitness and yield [90,103]. By contrast, priming is not associated with major fitness costs and has even been demonstrated to provide plants with a fitness benefit under conditions of pathogen attack [103,104]. Hence, priming for enhanced defence such as triggered by beneficial microorganisms could be a valuable tool for sustainable crop protection [105].

The signalling pathways that control ISR and plant defences against herbivores partly overlap [2,3]. Chewing insects are negatively affected by JA-mediated defences [25,46–49], and there is increasing evidence also that phloem feeders such as aphids and whiteflies are affected by JA-mediated defences [50,51]. Nevertheless, phloem feeders seem to activate the SA-signalling pathway that counteracts JA-dependent defences via crosstalk [50–53]. Because the plant hormone JA is of central importance in ISR and in plant defences against herbivorous insects, beneficial soil-borne microbes are expected to affect plant–insect interactions. Additionally, a recent study on the *spr2* tomato mutant (*Solanum lycopersicum*) which is impaired in JA biosynthesis has shown that the PGPR *Bacillus subtilis* can still induce resistance against whiteflies, suggesting that a JA-independent response is also involved [26]. Despite the relevance of unravelling the molecular mechanisms involved in plant defences to understand ecological interactions [3,25,27,28], to date very few studies have explored gene expression and signalling pathways activated in a microbe-induced plant after insect attack [25,26].

Effects on aboveground herbivores
Beneficial belowground microbes can induce plant resistance against aboveground insect herbivores, but simultaneously plants become bigger and more nutritive to certain herbivores. The final impact on insect performance will depend on the interplay between a positive effect derived from the enhanced plant growth and a negative effect derived from the induced resistance in the plant. Several biotic and abiotic factors can modulate such plant-mediated effects, which as a result can be positive, negative or neutral for aboveground insects (Table 1). Several factors still need further research. For instance, the effect of plant developmental stage which can influence plant defences against herbivores [54] should also be considered when studying microbe–plant–insect interactions [55].

In addition, microbe identity is a factor to investigate as there is evidence that the plant-mediated effects of microbes on aboveground herbivores are species-dependent, both in interactions with a single microbial species or with a microbial community [56–61]. For instance, different combinations of three species of the mycorrhizal fungus genus *Glomus* had different effects on host acceptance by a leaf-mining insect (*Chromatomyia syngenesiae*) and two seed-feeding insects (*Tephritis neesii* and *Ozirhincus leucanthemi*) [56]. In addition, in rice (*Oryza sativa*), a combination of different PGPR strains had a stronger negative effect on the performance of leaffolder larvae (*Cnaphalocrocis medinalis*) and on the activity of enzymes involved in plant defence (chitinases, trypsin inhibitors, polyphenol oxidase and lipoxygenase) than the same strains individually [57–59]. Studies that investigate more realistic situations that involve combinations of several microbial species are therefore needed, because the effects on herbivores and even on higher trophic levels can differ [60].

Abiotic stresses can also modulate the effect of the beneficial microbes [62,63]. For instance, the endophytic fungus *Acremonium strictum* enhanced whitefly (*Trialeur-odes vaporariorum*) mortality on tomato plants under drought stress conditions. Nevertheless, under standard water regimes the fungus had no effect on whitefly mortality [63]. Toxicity of metabolites produced by foliar endophytes on herbivores has been extensively reported [64], but the underlying mechanisms of the effect of root endophytic fungi on aboveground herbivores remains to be uncovered.

Plant genotype plays an essential role in plant-mediated interactions between microbes and insects [39,65]. The presence of *Rhizobium leguminosarum* in white clover (*Trifolium repens*) had a positive effect on the performance of the generalist caterpillar *Spodoptera exigua* [39], and this result was explained by an increase in plant biomass. When a different plant cultivar that produces defence-related cyanogenic compounds was used, the positive effect was neutralised. The authors proposed that the additional nitrogen gained from this symbiosis was used for the production of nitrogen-based secondary compounds, which could override the positive effect of the increased nutritional plant quality. The interaction between nitrogen-fixing rhizobia and legume plants is one of the best known examples of biological mutualism, but how this relationship affects aboveground herbivory has not been explored until very recently [39,66].

The outcome of microbe–plant–insect interactions can be dependent on the degree of specialisation of the insect [11,25,64,67]. Generalist insect herbivores are usually negatively affected by the toxic and deterrent metabolites of a certain plant species, whereas specialist insects are usually not affected and can even use such compounds to recognise their host plant [1]. Studies on *Arabidopsis* (*Arabidopsis thaliana*) show that the specialist caterpillar *Pieris rapae* was not affected by *Pseudomonas fluorescens*-mediated ISR (S.J. Zheng *et al.*, unpublished) [25], whereas the generalist *S. exigua* was negatively affected [25]. This negative effect was correlated with priming for enhanced expression of JA/ET-responsive, defence-related genes [25].

The effectiveness of microbe-induced defences is also dependent upon the feeding guild of the attacking insect herbivore [11,39,64,67]. Several plant secondary compounds such as glucosinolates and cyanogenic glycosides yield toxic products after hydrolysis by enzymes that are located in separate cellular compartments [1]. Such enzymes come in contact with the secondary compounds when plant cell contents are liberated during attack by chewing insects. Piercing–sucking insects insert their stylets intercellularly to reach phloem sieve elements. This feeding strategy allows phloem feeders to avoid bringing plant secondary compounds into contact with hydrolysing enzymes [68], and therefore they are less affected by these defences than chewing insects [11,39,64,67]. Taking into account the feeding guild and degree of specialisation of the insect, general patterns can be discerned in the effects of the interaction of plants with mycorrhizal fungi on insect herbivores: plant responses to mycorrhizal fungi seem to have a positive or neutral effect on the development of phloem feeders and specialist chewers, and a negative effect on mesophyll feeders and generalist chewing insects [11,64,67].

Effects on beneficial insects: natural enemies of herbivores and pollinators

Plants under herbivore attack emit complex blends of volatile organic compounds that attract natural enemies of the herbivore [4,52,69,70]. This is one of the main forms of indirect plant defence. The JA-signalling pathway is the most important signalling pathway involved in the emission of such volatiles [4,70], and multitrophic interactions that interfere with the JA-signalling pathway lead to changes in volatile blend composition [4,52]. Therefore, it is expected that beneficial microbes, which induce JA responses, will affect the composition or emission rate of such volatiles. Recently, the first example of a change in volatile emission for a microbe-induced plant in response to herbivory was recorded in which mycorrhizal plants emitted lower amounts of sesquiterpenes than non-mycorrhizal plants [71]. However, the consequences for indirect defence of such altered volatile emission by microbe-induced plants have not yet been evaluated.

Recent research shows that beneficial soil-borne microbes can mediate induced indirect plant defences against herbivorous insects and influence the effectiveness of the natural enemies of such herbivores (S.J. Zheng *et al.*, unpublished) [72,73]. Colonisation of plants by beneficial microbes can enhance the attack rate, performance and attraction of parasitoids [72,73] even when the number of herbivorous hosts is lower than on non-colonised control plants [59]. In those studies on the effect of beneficial microbes on indirect defences it is suggested that changes in volatile organic compounds trigger the attraction of the parasitoids, but this still needs to be verified.

Plant-mediated interactions can also occur between soil-borne microbes and insect pollinators, although only a few studies have been conducted thus far [74–76]. The studies available demonstrate an enhanced flower visitation [74–76] and seed set [75] of mycorrhizal plants compared to control plants. The underlying mechanisms reported include an increase in flower number, inflorescence size and nectar production [74,76], but whether plant volatiles are also involved remains to be uncovered. Pollinators are very important players in natural and agricultural ecosystems, and their integration in studies of multitrophic interactions has a high relevance and has only recently been initiated [77,78].

Effects of aboveground insect herbivory on beneficial soil-borne microbes

The effect of aboveground herbivory on belowground microbes has been much less studied than the reverse, but an emerging interest in the effects of aboveground herbivory on the interactions of plants with belowground organisms has been noted [11,65,79,80]. Insect herbivory can lead to a decrease of mycorrhizal colonisation [11,81–83], an increase [38] or it can have no effect [84]. In other cases, the change is not in the degree of colonisation but in the microbial community composition [65,82]. It has been proposed that at low or moderate levels of herbivory and in early stages of herbivory, a positive effect on mycorrhizal colonisation can be observed, whereas with a high level of herbivory and in later stages of infestation, a negative effect can be found [11,83].

The mechanisms underlying such interactions have hardly been explored, but it has been proposed that the main factor is the amount of carbon that plants allocate to the roots [11]. Aboveground herbivory usually causes an increase in carbon and resource allocation to roots, far from the damage. This is a mechanism that provides plants with the possibility to regrow when the herbivore pressure has decreased, a tolerance mechanism [6,80,85,86]. Additionally, such carbon allocation to roots after herbivory is plant age-dependent, reaching a minimum during the plant reproductive phase [55]. The actual mechanisms can be more complex because after aboveground herbivory plant defences and synthesis of secondary compounds are induced in the roots [6,87]. Furthermore, belowground microbes can act as pathogens under certain conditions [88,89] and the induction of broad-spectrum plant defences activated upon herbivore attack could also affect such microbes [90]. Nevertheless, empirical evidence of the mechanisms involved is needed.

In addition, aboveground herbivory can modify the quantity and composition of root exudates [8]. Root exudates play an important role in plant–microbe interactions in the rhizosphere [91,92], thus they might mediate the effect of aboveground herbivory on belowground microbes. Root exudates contain metabolites, such as carbohydrates and organic acids that stimulate bacterial mobility and the attraction of microbes to the roots [91,92]. For instance, *Arabidopsis* root exudates contained large amounts of malic acid after infection with a bacterial leaf pathogen, and this resulted in an enhanced attraction to the roots of the ISR-inducing microbe *B. subtilis* [91]. Taking all these examples together the aboveground–belowground interactions can be bidirectional, and possible feedback effects need to be considered in future research.

Concluding remarks and future perspectives

By addressing the integration of plant–microbe and plant–insect interactions, this review highlights that belowground microbes known to exert direct beneficial effects on plants can affect the interactions of plants with various community members aboveground. The mechanisms involved in microbe–plant–insect interactions include plant growth promotion and induced defences against herbivores, and the interplay between both effects will determine the final impact of herbivory. The effect of microbial induced systemic resistance against microbial pathogens has been studied for many years, but relatively little is known about the effect of ISR on herbivorous insects. Transcriptomic and metabolomic approaches are promising to advance this field.

Inducing resistance against herbivores is not the only mechanism through which soil-borne microbes affect plant–insect interactions. Enhancing the effectiveness of natural enemies can also decrease herbivore pressure, and there is evidence that microbes can enhance such effectiveness. But even if the direct and indirect defences fail and the herbivore pressure increases, soil-borne microbes can enhance plant biomass and yield, increasing plant tolerance. Additionally, the attraction of other beneficial organisms to plants colonised by beneficial microbes, particularly pollinators and natural enemies

of herbivores, should be the focus of more attention in future research.

Beneficial microbes have interacted with plants for millions of years and, by modulating the interactions of plants with their attackers, beneficial microbes have probably contributed to plant diversification. Because plant genotype is an essential factor affecting mutualistic interactions, plant breeders might want to include traits that promote beneficial plant–microbe interactions in their selection process. Although beyond the scope of this review, it should be pointed out that some of the beneficial microbes reviewed here have also other beneficial effects such as disease suppression via microbial competency or biological control of pests and pathogens [93]. Microbes can provide a promising contribution to sustainable pest control in a changing environment, through enhancing plant productivity, resistance to pathogens and pests, attractiveness to beneficial insects and tolerance to abiotic and biotic stress. The aim of this review is to contribute to an intensified development of the field of microbe–plant–insect interactions through combining different approaches at several levels of biological integration, and taking into account the bidirectional nature of aboveground–belowground interactions.

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